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BIOLOGICAL BULLETIN

POWER OF RECOGNITION AMONG ANTS.

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WITH PHOTOGRAPHIC ILLUSTRATIONS BY MR. J. G. HUBBARD AND
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When power of recognition is to be tested, appeal for evidence of that power is properly made through the leading sense. We should take evidence from the eagle through its sense of sight, from the mole through its sense of hearing, from the caterpillar through its sense of touch, from the ant through its sense of smell.

That ants have associative percepts which are independent of their chemical sense, is proven by their behavior. Ants learn to be unafraid of the light from which they instinctively withdraw their young.¹ When ants are put into an artificial nest, some weeks are required for their making acquaintance with their domicile, but after such acquaintance has been perfected, they may be transferred to a replica of their abode, whether it be a Petri cell, a glass house, or a wooden box, and they will be wholly at ease in it, and will quietly resume their accustomed routes over its floors or withdraw into it from a strange environment, although it lacks their nest-aura.

I divided a small colony of *Camponotus Pennsylvanicus* into two sections. I fed and fondled the members of the one section until they manifested a sense of safety in my presence, would mount my finger and make a leisurely promenade upon my hand or would return to me after an hour's wandering in my room. These ants not only ceased from biting me when I took them upon my hand, but became so tame that they would

¹ "Supplementary Notes on an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, September, 1903, p. 493.

remain quiescent in their Fielde nest¹ for some minutes after the roof-pane had been lifted.

Upon the ants of the other section I practiced such atrocities as that of lifting them frequently by the leg with a pair of forceps or plunging them for an instant in cold water. The ants of this section quickly acquired such associations with the lifting of their roof-pane, that they fled through the compartments of their house in wild panic whenever I touched the glass.

PRELIMINARY STATEMENTS.

Is is the purpose of this paper to show that ants have power to recognize certain ant-odors after months or years of separation from those identical odors, and in order that the evidence presented may be plain, it appears necessary to first restate certain facts, well established by past experiments.

1. Ants of different species in different communities or colonies, and also ants of the same species and variety in different communities or colonies, ordinarily show aversion to each other on meeting, and are especially truculent in defense of their young. The cause of this general and perpetual feud among ants of different colonies, is due to difference of odor, discerned through their antennæ, their organs of smell. Fear and hostility are excited in the ant by any ant-odor which she has not individually encountered and found to be compatible with her comfort.

2. If ants of different species, or even of different genera or subfamilies, are made pleasantly acquainted with each other within a few hours after hatching, they will thereafter continue to live together in amity, constituting a mixed colony.² The acquaintance thus formed is individual, and every ant, in her later behavior, will act in accordance with individual experience. Acquaintance with the odor of one species or colony does not secure from the experienced ant an amicable reception of a representative of any other species or colony.

Among the mixed colonies, formed by me in August, 1903, twenty *Stenammina fulvum* workers lived with a *Cremastogaster lineolata* queen a full year, and the harmony of the nest was as

¹ Described in BIOLOGICAL BULLETIN, Vol. II., No. 2, 1900, and Vol. VII., No. 4, 1904.

² "Artificial Mixed Nests of Ants," A. M. Fielde, BIOLOGICAL BULLETIN, Vol. V., No. 6, 1903, p. 320.

complete as if its inmates had been of one species. Representatives of three subfamilies, *Formica subsericea*, *Stenamma fulvum*, and *Stigmatomma pallipes* lived amicably together five months before the last Ponerine ant died, leaving the Camponotine and the Myrmicine ants to continue together a full year. *Formica lasiodes*, *Lasius latipes*, *Stenamma fulvum*, *Myrmica rubra* and *Cremastogaster lineolata* affiliated through several weeks. All these and other mixed colonies continued until they were disintegrated by me, and friendly treatment was accorded in them to all introduced ants bearing a familiar and therefore an approved odor, while hostile attack was made on every ant bearing an unfamiliar and therefore a disapproved odor. An enlarged acquaintance with ant-odors did not render any ant tolerant of unknown ant-odors, and in no established mixed colony was an ant of any other than the already represented colonies permitted to live, even when the introduced ant was of the same variety.

I have at the present time a mixed colony of *Camponotus pictus*,¹ *Formica subsericea*, *Formica lasiodes*, and *Stenamma fulvum*, and although there are no young of any species in their nest, they have killed every one of several newly-hatched *Cremastogasters* that I have introduced, and they allow none of the latter species to live when hatched in their nest from introduced pupæ.

3. Ants inherit odor from the queen from whose eggs they are developed. That the queen endows her eggs with an odor, and that newly-hatched queens and workers have an odor recognized by their queen-mother, is proven by the fact that an ant may be isolated from the pupa-stage until it is some days old, never having smelled any ant-odor beside that of its own body, and it will instantly snuggle its queen-mother at first meeting, although it may attack other queens, or sister-workers much older than itself. I have known a young worker to identify its mother among five queens of its species presented for its examination. The queen doubtless recognizes her own odor in the callow that she has never before met.

As I have to present the results of several experiments in which the N colony appears, it will be well to here give some

¹ I am indebted to Dr. William Morton Wheeler for kind identification of *Camponotus herculeanus pictus*, and of *Formica pallide-fulva*. A single ant of the last-named species lived for a year in one of my artificial nests with many *Formica subsericea*.

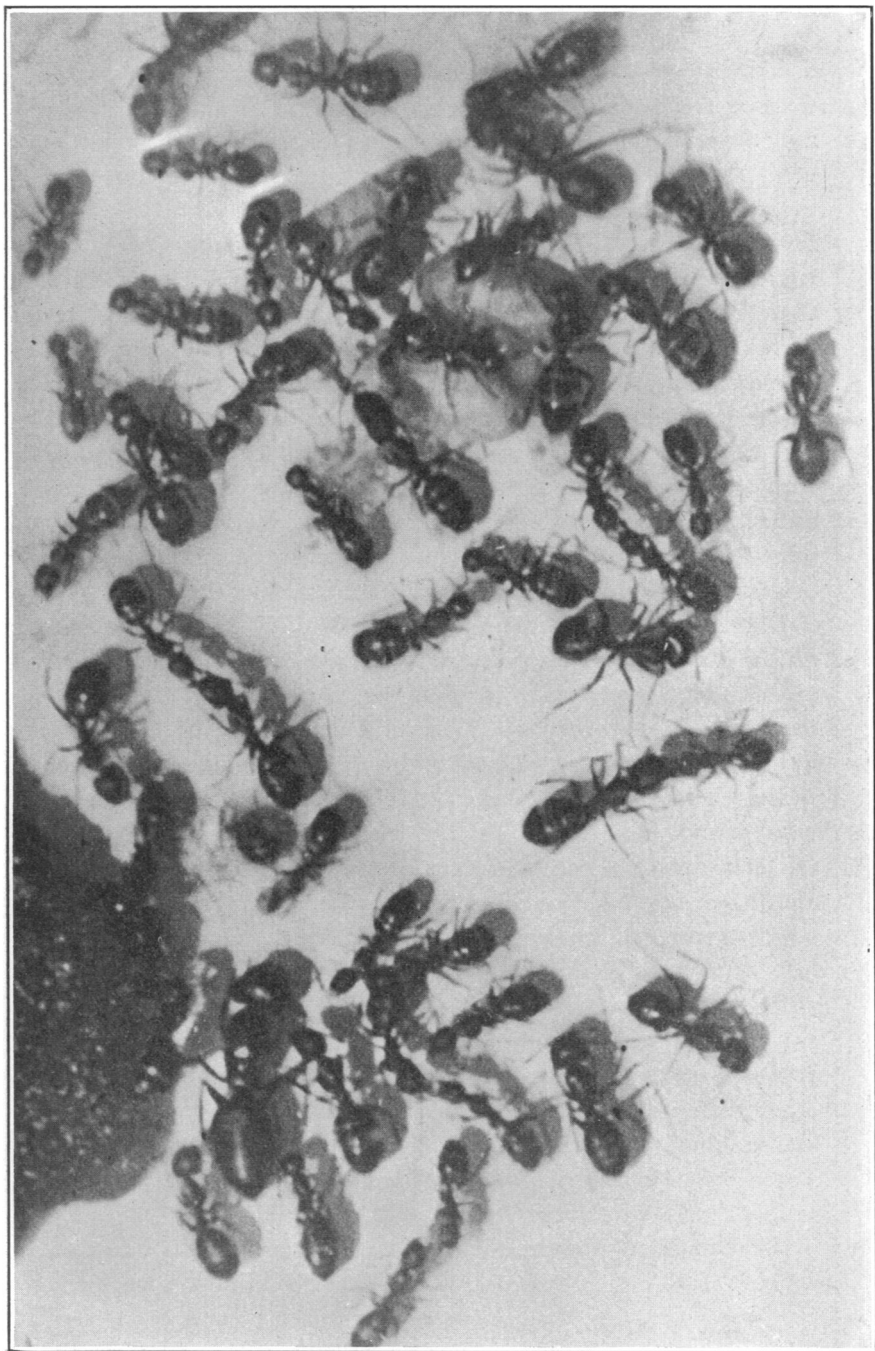


FIG. 1. *Camponotus pennsylvanicus*. Somewhat magnified. Actual length of queen 2 centimeters.

account of that colony. On July 28, 1903, this N colony of *Camponotus pennsylvanicus* was captured on Nonamesset Island, and was housed in a large Fielde nest. It consisted of a queen two centimeters long, some scores of workers, and numerous cocoons. During the first week in August, 1903, the queen deposited about one hundred eggs, and then ceased laying until the following March. The first larva from the August eggs was observed on August 27. From these larvæ the first cocoon appeared on March 13, 1904. On April 8, 1904, there were many large larvæ in the nest, and there were numerous cocoons varying in length from five millimeters to thirteen millimeters. The first cocoon of this brood hatched on April 24, the temperature of the room being 24° C. or 76° F. These cocoons continued to hatch, most of them in carefully segregated groups, until July 14, when the last cocoon rendered its callow.

Experiment A.—Three large workers hatched each in isolation on July 8, 11 and 14, 1904, from the August eggs of the N queen. On August 5, these three worker-ants, ranging from twenty-two to twenty-eight days in age, and never having met any ant-queen, nor any ant older than themselves, instantly affiliated with their queen-mother, and with each other, at the first meeting. The queen manifestly recognized the odor borne by the callows, and at once snuggled with them.¹ They each recognized in her and in each other the only ant-odor they had ever known, that of their own bodies.

Experiment B.—Four N colony workers, the issue of eggs deposited by the queen in August, 1903, were hatched from segregated cocoons, between May 15 and June 15, 1904. On July 6, when the age of these ants ranged between twenty-one and fifty-two days, and they had never met any other ant of their species, I introduced their queen-mother to their nest. The five immediately affiliated and the previously introduced larvæ were brought and placed beside the queen. The queen must have been at least one year older than these workers, and the workers must have recognized in the queen their own odor at hatching time.

Experiment C.—Five *Camponotus* workers hatched between

¹ The behavior of the ants in these experiments was observed through an orange-tinted roof-pane, under which the ants behave as if in darkness. See "Supplementary Notes on an Ant," referred to in first foot-note.

April 25 and May 10, 1904, out of cocoons from the August eggs of the N queen. They were from fifty-seven to seventy-two days old, and had never met other ants of their species, when on July 6, 1904, I introduced to their nest their queen-mother. Within five minutes the queen had touched antennæ with every worker and had become the center of a friendly group.

Experiment D. — Fourteen *Camponotus* workers hatched on or after April 24, and on or before May 10, 1904, out of cocoons from eggs laid by the N queen the preceding August. They had never met other ants of their species, when on July 6, 1904, the oldest of the segregated group was seventy-three days old, and I introduced to their nest their queen-mother. There was for an instant great excitement in the nest, and some tentative nabbing of the queen; but in less than one minute the workers had discovered that she was their own. Within a few minutes, four of the workers had licked the queen, one had stood upon her back, and seven others had grouped themselves close about her.

The behavior of these workers toward their queen indicates that her odor is an unchanging one, or that if there be a change in her odor it is but slowly effected.

The behavior of these ants toward their queen was markedly unlike their behavior toward their sisters, when great diversity in ages was represented.

4. Worker ants change in odor as they advance in age,¹ as was shown by experiments made by me in 1902. Further evidence of this fact will be offered later in this paper. Forty days may pass with no change so great as to elicit from former acquaintances any expression of suspicion or antagonism, but in other cases from forty to sixty days so differentiates the known odor as to inhibit association between the ants.² This suspicion

¹ "Notes on an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, December, 1902, p. 609. Also "Cause of Feud Between Ants of the same Species Living in Different Communities," A. M. Fielde, *BIOLOGICAL BULLETIN*, Vol. V., No. 6, 1903, p. 327.

² All the ants employed in the experiments recorded by me have been under my constant care and my frequent observation. No person beside myself has ever had access to them. They have spent the summers, from the first of June to the end of September, at the Marine Biological Laboratory, Woods Holl, Mass., and the remainder of every year in New York City.

or antagonism is always shown¹ by the younger ants, toward the older, if the ants be of the same colony, and if the young ants have been guarded from association with ants older than themselves.²

Experiment E. — On July 18, 1904, I put into the nest of two segregated workers of the N colony, hatched from cocoons taken from the wild nest July 28, 1903, and at the time of this ex-

¹ In all experiments here recorded, unless a contrary condition is indicated, the ants whose recognition of a visitor was in question had in their nest inert young that had engaged their attention during several previous days. The action of resident ants toward a visitor is much more prompt and decisive when there are larvæ or pupæ in the nest.

² In experimenting with ants, a third source of individual odor, not set forth in this paper, although always reckoned with in the experiments, lies in the other ants with which the individual associates. This odor appears and disappears with certain external conditions. Ants take on the odor of their associates in a mixed nest, and this incidental odor usually disappears after about ten days of isolation, the inherent odor then reasserting itself. Ants may be smeared with the juices of ants of another species or colony and may thereby become immediately subject to attack from comrades from whom they have been but momentarily removed.

I have lately submerged ants for eighty hours or more in distilled water at a temperature of 10° C., putting two species or two colonies into the same water, using thirty-five cubic centimeters for a dozen ants, and I have found that the ants of each species or colony, when revived and returned to their former nest, were attacked as are enemies, and that ten days proved to be an insufficient time for the reassertion of the inherent over the incurred odor. That these attacks from comrades were due to the alien odor acquired in the water and not to some other cause, was shown by the fact that when similar ants were likewise submerged in unmixed groups, the returned ants were amicably received by their former comrades.

I thus submerged, in thirty cubic centimeters of water, three *Camponotus pictus* and fifteen *Stenamma fulvum*, for eighty hours. One of the *Camponotus* revived, and a day later I returned it to its three former comrades, employed in the care of cocoons in a small Fielde nest. The three instantly attacked the one, and would doubtless have slain it had I not interfered. Having rescued, I isolated it for ten days in a Petri cell, and then again returned it to its former nest. Two of the three resident ants at once attacked and killed it. Of the *Stenammæ* several revived, and on my returning them to their former nest, they were all killed by their quondam associates.

Of four *Stenammæ* that revived and recovered after eight days submergence in company with five *Camponotus pennsylvanicus*, three were killed by former comrades on my returning them to their nest. One of the four was isolated by me, in a Petri cell, for twenty days before I returned her to the nest, and there the returned ant was for some minutes the center of an examining circle of many ants. A day later she was being dragged by two workers, but she was ultimately restored to good standing in the nest.

It is interesting to observe the puzzled or critical demeanor of an ant engaged in ascertaining whether a new-comer has an incurred or an inherent foreign odor.

periment eleven months old, a callow of the same colony, just seven days old. The callow received careful examination from the older ants, and was then amicably entertained by them. They doubtless recognized in the callow their own early odor.

Experiment F.—On July 6, 1904, after the queen and the fourteen workers mentioned in experiment D were all serenely grouped in the nest there described, I introduced two workers¹ of the N colony, hatched between August 14 and September 3, 1903, and therefore about ten months old, while the resident ants were not over seventy-three days old. The two visitors had affiliated previously with the N queen, and had been approved by her. They were probably the issue of her eggs of the previous year. They were, however, seven or eight months older than the resident workers, and, although they were larger than any worker resident, they were persistently attacked and dragged, sometimes by more than one resident at a time. The visitor-ants did not retaliate. One of them tried to placate her young sisters by offers of regurgitated food, and after a half hour there were signs of diminution in the strength of the attacks. I then removed the visitor-ants. There are all degrees in the hostility shown by ants to one another, as well as many variations in the degree of closeness in their affiliations.

In this experiment, the older ants had met no younger ones during their lives, and the younger ones had never before encountered sisters older than themselves.

RECOGNITION OF ODORS OF OTHER SPECIES.

The A Series.

Evidence of ability to recognize odors that have not been encountered during many months has been taken from ants of diverse species and of a recorded life history. In August, 1903, I formed a mixed colony of workers of *Camponotus pennsylvanicus*, *Formica subsericea* and *Stenamma fulvum*, all of whom hatched in my artificial nests between August 14 and September 3. Every ant within a few hours after its hatching was

¹ My method, which is also Forel's, of marking ants so as to readily distinguish them from others of their species, is described in a foot-note of "Notes on an Ant," already referred to. Ants were marked whenever an experiment required it.

made acquainted with every predecessor in this mixed colony and no discord appeared in the new nest. This mixed colony was marked A. On September 24, when none of these ants was less than twenty days old, and none more than forty-one days old, I separated them according to genera, putting the *Camponotus*, the *Formicas* and the *Stenammæ* each into a Fielde nest that was new and therefore had nonest-aura. The nests were respectively marked A1, A2 and A3. No young was permitted to hatch in any nest, but inert young from the workers' eggs, or introduced larvæ from other nests were always present when tests of recognition were to be made as severe as possible. No ant of any species was admitted to either of the segregated groups except as recorded in the experiments.

Nest A1. — On April 8, 1904, there were in the *Camponotus* nest,



FIG. 2. *Stenamma fulvum*, with larvæ and pupæ; slightly magnified. Actual length 5 to 7 mm.

marked A1, three large and vigorous workers, without young. I then introduced two Stenammias that the Camponotus had known in the previous September in the A nest. The Stenammias manifested terror and the Camponotus made instant and violent attack upon them, so that I intervened in the ensuing battle, saved the lives of the Stenammias, and returned them to their own nest. It was evident that during the six and a half months of separation these ants had changed in odor, and that the odor borne by them in April was unknown to the ants with whom they had associated in the previous September. I was unable to offer to this group A1 the companionship of young Stanammias having the same odor as had their former associates at the time of association, and young Stenammias taken at a later date from the wild nest in the summer of 1904, were always killed by them. The Formicas were likewise rejected.

Nest A2.—The Formicas that had lived, none less than twenty and none more than forty-one days, in nest A, were domiciled in nest A2. They had been separated from the Camponotus six and a half months, when on April 8, 1904, I introduced into their nest, where there were twenty-six workers and no young, a Camponotus from nest A1, comrade of their earliest days. The Formicas immediately attacked the Camponotus, and I removed the latter to save her life. Six month's progress in odor formation had carried her outside the acquaintance of her former associates. The same antagonism was manifested toward the other two residents in nest A1.

These Formicas continued to reside in their nest and had laid a few eggs, which were under their care when on April 25, 1904, I introduced to their nest three Camponotus newly hatched from eggs that were laid in August, 1903, by the queen-mother of the Camponotus in nest A1. These young Camponotus received amiable welcome from the resident Formicas, and during the next ensuing days, to May 10, I added several more callows. The Formicas, now eight months old, continued to live amicably with the young Camponotus, whose odor had been known to them in their earliest days. They regurgitated food to the young ants, permitted them to carry the egg-packet and care for the larvæ, and in all respects treated them as if of their own colony. There

was no death in the nest for twenty days after the introduction of the young *Camponotus*, but I removed them on June 25. *The Formicas recognized, after seven months of separation from it, an ant-odor previously known to them.*

I was unable to introduce to this nest any young *Stenammass* that the *Formicas* would accept, as I could command none of the same lineage and age as those known to them in the autumn of 1903. The individual *Stenammass* in nest A₃, with whom they had formerly associated in the A nest, were now of another odor, and the *Formicas* refused to affiliate with them.

Nest A₃. — The *Stenammass* in this nest had lived in nest A, none less than twenty and none more than forty-one days, and since September 24, 1903, they had met no ant other than those in their own nest. On April 8, 1904, I introduced into their nest, where, there were forty-one workers, a former comrade, a *Formica* from nest A₂. She was fiercely attacked, and I removed her. Other *Formicas* from the same nest were likewise attacked. I then introduced *Camponotus* from nest A₁, and they were received with like animosity. It was instantly made evident that the resident *Stenammass* found in every visitor an unfamiliar odor. I removed each visitor as soon as her status among these *Stenammass* had been made plain, and the A₃ nest remained quiescent until April 24, when I introduced a day-old *Camponotus*, the issue of an egg laid the previous August by the mother of the rejected individual in nest A₁. Within a few minutes after its introduction, three of the *Stenammass* had licked the *Camponotus*, and all the *Stenammass* had viewed it with approval. It was taken care of as tenderly as if it had been a *Stenamma* calow. On the same day I added two newly hatched *Camponotus* of the same lineage, and they were kindly entertained until April 27, when I removed them to another nest of *Stenammass*, the M nest. These M *Stenammass* were of the same age and colony as were the *Stenammass* in nest A₃, differing from them only in never having lived with *Camponotus*. There were also about the same number of resident ants. As soon as I introduced the *Camponotus* into the M nest, the *Stenammass* attacked them, and although they were double the size of the residents, and of tougher integument, the residents harried them to death. The

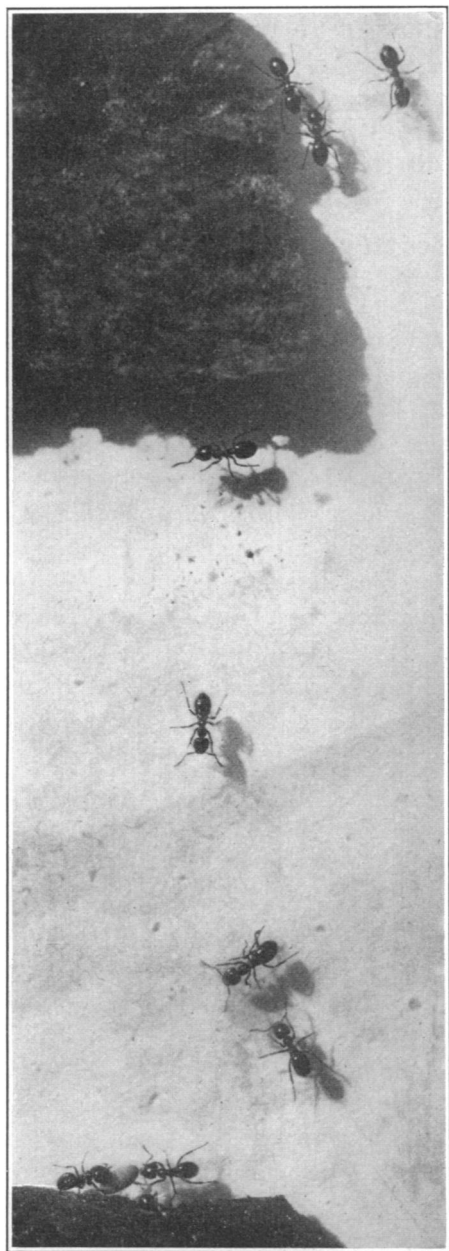


FIG. 3. *Lasius latipes*, magnified. Actual length 5 millimeters.

behavior of the M ants indicates that that of the A₃ ants was based on a recognition of odor, and that the *Stenamma's* power of recognition extends through an interval of at least seven months.

The B Series.

Another series, marked B, was also established, having its beginning on July 20, 1903, additions of newly-hatched workers being made to the mixed colony up to August 28, or during a period of forty days. The B mixed colony consisted of *Stenamma fulvum* of the C colony, *Lasius latipes* of the F colony, and *Cremastogaster lineolata* of the H colony. On September 24, 1903, I separated these ants according to genera, segregating each genus in a new Fielde nest, marked B₁, or B₂ or B₃, where it remained until the end of the recorded experiments, with no other ants than those here mentioned ever introduced or permitted to hatch in its nest.

Nest B 1. — On April 1, 1904, over six months after their segregation, there were in the B1 nest about sixty *Stenammas*. I then introduced to their nest two *Lasius*, their former comrades, taken from nest B2. No fear was evinced by the *Lasius*, and no aversion by the *Stenammas*. Residents and visitors perfectly affiliated, and the two *Lasius* remained safely in the B1 nest four full days. I then, on April 5, removed the two *Lasius*, and put them into a nest of *Stenamma fulvum* where there were two queens and sixteen workers, all hatched in August, 1902, and therefore a year older than were the ants in nest B1. They were from the same C colony, but had never associated with *Lasius*. In this nest the *Lasius* tried to flee or to hide, behaving as do ants when in a nest of recognized enemies. At first they eluded the *Stenammas*, but when I again examined the nest, on the evening of the same day, both *Lasius* had been killed and put on the rubbish-heap.

It appears that these very strong-smelling ants, the *Lasius*, had not so changed their odor during six months that the B1 *Stenammas* did not recognize it. But on June 11, 1904, I took from the wild nest of the F colony two *Lasius* workers, of unknown age, and introduced them into the B1 nest of *Stenammas*. They were soon killed, and two like them were also killed when introduced on the ensuing day.

On August 11, 1904, I introduced a newly hatched *Lasius* from the R colony, and it was at once killed.

On June 11, 1904, I sought in the old wild nest of the *Lasius* F colony for a remainder of its population, and secured a few workers and four larvæ. On August 4, three cocoons and one naked pupa had appeared from these larvæ, and from these cocoons the first worker hatched on August 18. It was immediately put into the B1 nest, where it appeared as a yellow pigmy among brown giants. It was much patted with the antennæ, was licked, and was cared for among the eggs, larvæ and pupæ over which the *Stenammas* were strenuously engaged. *The Stenammas recognized an odor from which they had been eleven months separated.*

The *Stenammas* of nest B1 met no *Cremastogaster* from September 24, 1903, until July 7, 1903, when I introduced into their

nest, occupied by fifty of the old residents, with larvæ from their own eggs, several newly-hatched *Cremastogaster lineolata* from a wild nest V. Within a day all these young *Cremastogasters* had been killed and their bodies piled together in a corner of the food-room. Others of their kind met a like fate on July 9.

On the 24th of June, I had happily secured some larvæ, with workers to rear them, from the wild nest of the old H colony of *Cremastogasters*, and on July 22, I put a dozen callows, newly hatched from this stock, into the B1 nest, where the residents were much engrossed with their own pupæ. Two or three of these introduced callows were killed and dismembered, while all the rest were accepted into close companionship by the resident *Stenammas*. The *Cremastogasters* were permitted to walk over or rest upon the pupa-pile, they were gently licked, and none was harmed during the ensuing twelve days. I then removed them to prepare the nest for another experiment.

But while the *Cremastogasters* were still in the B1 nest, on July 25, I introduced a newly hatched *Formica lasiodes*, in order to see whether these *Stenammas* would accept a callow of unknown odor. This visitor was immediately killed and carried to the rubbish-pile.

Further evidence that the *Cremastogasters* were offspring of the queen that laid the eggs from which the B3 *Cremastogasters* issued, was obtained by putting some of them into K nest with an H colony queen that had never before met any *Cremastogaster* workers of any colony, having spent her whole life since she was hatched in August, 1903, with *Stemma* workers. This queen and the *Stemma* workers with her, all accepted the H colony *Cremastogaster* workers hatched in the latter part of July, 1904, and continued to closely affiliate with them. They were doubtless of the same odor as was the queen in this K nest, being progeny of the same queen in different years, the queen in K nest still retaining her queen-mother's odor, while the worker-callows bore the queen-mother's odor as yet unchanged by ageing.

Stemma fulvum in my artificial nests, when they had no young of their own, have many times permitted *Cremastogaster* pupæ to hatch in their nest and to live there among them. But

when engaged in the care of their own young, they have, unless previously acquainted with *Cremastogasters*, always killed the *Cremastogasters* as soon as the latter hatched and began to move about. It appears that the *Stenammes* of nest B1 recognized an old acquaintance in the young *Cremastogasters* of the H colony, and resumed toward them their accustomed behavior. In other words *the Stenammes recognized an odor after an interval of ten months in which that odor had not been encountered.*



FIG. 4. *Cremastogaster lineolata*; magnified. Actual length 5 millimeters.

Having removed all *Cremastogasters* from nest B1 on August 4, there followed an interval of twelve days in which they had met no *Cremastogasters*. Then on August 16, 1904, I introduced to their nest one of their old comrades in nest B, a *Cremastogaster* from whom they were separated on September 24, 1903. This visitor was killed by them within a few hours. In less than eleven months she had attained an odor unknown to them.

Nest B2. — There were in April, 1904, so few of the *Lasius* in this nest that I gave their power of recognition no test within their own nest. All of them were used till their extermination, in the experiments in nests B1 and B3.

Nest B₃. — On April 5, 1904, over six months after the segregation of the *Cremastogasters*, there were about fifty workers in their nest, B₃. I then introduced two *Lasius*, with whom they had lived in amity some forty days, and from whom they had been separated over six months. The residents attacked the visitors from nest B₂, and would have slain them had I not rescued them. There was no room for doubt concerning the absence of recognition among the *Cremastogasters* of the present odor of the *Lasius*, ants presenting an odor so strong that a single one of them is very impressive to human nostrils. I was unable at that time to introduce to these *Cremastogasters* any *Lasius latipes* younger than were those with whom they had formerly associated. But on August 12, 1904, when I introduced a newly-hatched *Lasius latipes* of the X colony, they immediately killed it. On August 20, 1904, I introduced a young *Lasius* from the wild nest of the F colony, a sister of the one put on the 18th into nest B₁. This ant was amiably received. *The Cremastogasters recognized an odor from which they had been eleven months separated.* On the same day, August 20, 1904, I also introduced an adult *Lasius*, of unknown age, but also of the F colony, one of the nurses of the newly-hatched ant already accepted. This adult *Lasius* was killed during the ensuing night.

On April 8, 1904, I introduced to these *Cremastogasters*, in nest B₃, two of the *Stenammas* with whom they had pleasantly lived for forty days, in the preceeding autumn, and from whom they had been separated more than six months. One of the visitors behaved as if in an alien nest, showing fear and attempting to escape. The other fought with a resident. Absence of recognition on either side indicted such change of odor during the period of separation as to render these ants unacquainted with one another.

Early in July, 1904, I was able to introduce to this nest several newly-hatched *Stenammas* from the wild nest of the C colony, kindred of the ants in nest B₁. There were many queens in that wild nest. That the callows might not bear the odor of older ants, I segregated some pupæ, and offered the callows newly hatched therefrom to the ants in nest B₃, but these callows were all killed and dismembered within a few days after

their introduction. They were doubtless the progeny of other queens than those which produced the early acquaintances of the *Cremastogasters* in nest B₃.

HYPOTHESIS.

From such data as is here presented, correlated with records of past years, it is possible to diagrammatically represent the probabilities that an ant, isolated from the pupa-stage, would encounter a known odor at a first meeting with another ant of her colony. If the odor of a queen be unchanging, if she impart odor to all her eggs, if that odor be perceptible in the inert young, and if from the beginning of the active life of the worker there be a progressive change in the inherited odor borne by her, then from each summer's deposit of the queen's eggs there would be in the following summer more than one odor among the workers, because all the eggs of a queen are not hatched during the summer in which they are deposited. We may suppose a young, fertilized queen, the founder of a colony, to deposit eggs in her isolated cell in July, and to have reared her first small brood in not less than sixty days.¹ The eggs laid by her in the latter part of summer or early autumn would reach the larval stage in late autumn, and in that stage would be carried over to the next June, to hatch as ants in summer. While this second brood was developing, the first brood would have advanced to the odor of ants many months old. Their odor would then be unknown to an ant newly hatched from the queen-mother's egg and having the odor of its own body as its only criterion of ant-odor. Succceeding years would bring similar conditions.

In Sir John Lubbock's nests, one ant-queen lived to her fourteenth, and another to her fifteenth year; but the purpose of the diagram is reached by the supposition that the queen lives ten years.

¹ For time of incubation of eggs, larval period and pupa-stage in *Slenamma fulvum*, see "A Study of an Ant," A. M. Fielde, *Proceedings of the Academy of Sciences of Philadelphia*, September, 1901, p. 430. The time of incubation appears to be twenty days for all ants that I have observed; the larval period may be extended to at least one hundred and forty days in a high temperature, and probably to a much longer time in cold weather; and the pupa-stage occupies about twenty days. I have known the larval period to be passed in twenty days.

Diagrammatic representation of the progressive change of odor in worker-ants.

The arabic numerals, in horizontal line, indicate successive years in the life of a queen, the founder of a colony.

The Roman numerals at the left hand, denote successive broods from the eggs of this queen, here supposed to be the only fertile female of the colony.

The letters are used as symbols of the odor of worker-ants of this colony.

	1	2	3	4	5	6	7	8	9	10
I.....	a.....	b+a	c+b.....	d+c.....	e+d.....	f+e.....	g+f.....	h+g.....	i+h.....	j+i
II.....	a.....	a.....	b+a.....	c+b.....	d+c.....	e+d.....	f+e.....	g+f.....	h+g.....	i+h.....j+i
III.....	a.....	a.....	a.....	b+a.....	c+b.....	d+c.....	e+d.....	f+e.....	g+f.....	h+g.....i+h.....j+i
IV.....	a.....	a.....	a.....	a.....	b+a.....	c+b.....	d+c.....	e+d.....	f+e.....	g+f.....h+g.....i+h.....j+i
V.....	a.....	a.....	a.....	a.....	a.....	b+a.....	c+b.....	d+c.....	e+d.....	f+e.....g+f.....h+g.....i+h.....j+i
VI.....	a.....	a.....	a.....	a.....	a.....	a.....	b+a.....	c+b.....	d+c.....	e+b.....f+e.....g+f.....h+g.....i+h.....j+i
VII.....	a.....	a.....	a.....	a.....	a.....	a.....	a.....	b+a.....	c+b.....	d+c.....e+d.....f+e.....g+f.....h+g.....i+h.....j+i

If all the ants from this queen's seventh year eggs and having the *a* odor were segregated from their pupa stage, onward, the only ants of this colony with which they would affiliate on meeting would be such ants as were hatched in her seventh year from eggs laid by the queen in her sixth year. If groups of such ants were segregated they would, if hatched less than forty days apart, affiliate on meeting.

Ants of the *b*, *c*, *d*, *e*, *f* and *g* odors would affiliate with ants of the *a* odor, because that odor was once familiar to them in their own bodies. It would be a recognized odor.

The conditions of odor in her colony during her lifetime are crudely and only approximately represented by the diagram, but the representation conduces to an understanding of certain phenomena observed by me in the C colony, which I have now studied four years, in its natural nest, and in my artificial ones.

When queens, instead of flying away to found new colonies, remain in the colony where they hatched and increase its population by their progeny, there is opportunity for all the members of that colony to receive a liberal education of the chemical sense. Every ant acts on individual experience, and if its experience be narrow it will quarrel with many, while acquaintance with a great number of ant-odors will cause it to live peaceably with ants of diverse lineage, provided the odors characterizing such lineage and age environ it at its hatching. If some of the workers were separated from their colony in their youth, and kept segregated several years, the sequestered ants could amicably meet younger ants from their old home nest only by an act of memory, or a power of recognition spanning the interval of their separation from their colony. Precisely this condition has been created by me with ants of the C colony.

The C colony is a great community of *Stenamma fulvum* that lives under stones scattered at considerable intervals over an area ninety yards in diameter, along a lane and pasture. I have been unable to find any other colony of *Stenamm*as in its vicinage. Many of its young queens appear to mate with their kin and remain in the colony. I have found as many as fourteen deälated queens in a single shovelful of its nest-earth. The queens and workers from its extreme limits always affiliate unhesitatingly on meeting within its domain.

On August 22, 1901, I took from under a central stone of this colony queens, males and workers, and divided them into two sections, each of which was kept segregated in a Fielde nest for two years. No young was permitted to hatch in either section, and when I united the two sections in August, 1903, they affiliated instantly, and also affiliated less perfectly with queens and workers freshly brought from the wild nest.¹ I kept the ants of

¹ Detailed account of these meetings may be found in "Cause of Feud between Ants of the Same Species," already referred to, p. 328.

the two united sections, again without young, another year, until August, 1904, when I introduced to their nest marked queens and workers from their old wild nest. Of the two queens introduced one was at once received into full fellowship. The other was simultaneously licked and dragged by different worker-residents, but was accepted at the pupa-pile within a few hours. The workers introduced had kindly reception. Of one hundred and fourteen callows introduced one by one, or a few at a time, an interval of repose being given between the removal of one and the introduction of its successor, only two were attacked. While it is true that all the accepted callows of the summer of 1904 might have had the odor of the resident queen, it appears more probable that most of them *bore odors that were recognized by the resident workers after the lapse of three years.*

These ants had certainly not within their three years of segregation met a two-year-old or a one-year-old ant of their colony, from outside their artificial nest. In August, 1902, I segregated a queen and workers all hatched during that month, and in August, 1903, I likewise segregated a newly hatched and similar group. All these ants were of the C colony, and no young was permitted to hatch in any of these groups, each in its artificial nest. In August, 1904, I therefore had command of ants of the C colony, one group in the C nest, consisting of ants brought in from the wild nest on June 24, 1904; one group C₁, just one year old, one group C₂, just two years old, and one group C₃, three years old or more. All had been acquainted with their seniors before segregation. In August, 1904, the three-year-old ants received amiably, within their nest, ten of the two-year-old ants, and ten of the one-year-old ants, indicating a perfect recognition of odors no longer represented in their own nest, and from which they had been long separated.

On the other hand, when I introduced the three-year-old ants, queens or workers, into a nest populated with hundreds of workers taken in June, 1904, from the wild nest or hatched within that nest during the present summer, the three-year-olds were always fiercely attacked. *They had become an alien colony to the younger generations of their former wild nest.* The C colony has been much harried in its natural domain, by the rebuilding

of stone fences, by repairing of the lane-road, and by my own depredations. Ants so old as my three-year-olds have apparently become almost unknown in the wild colony.

The older the colony, the fewer would be the chances that any ant, segregated as a pupa and always kept in isolation, would find its own odor in any ant taken at random from the nest from which said pupa had been taken. In August, 1904, I thus isolated pupæ and the ants hatched therefrom, and from among many experiments made with them, I record the following as typical: I isolated a pupa from the C colony wild nest, and when the ant that hatched from it was eleven days old, never having smelled any ant-odor other than that of its own body, I introduced one by one to its Petri cell, where it was engrossed in the care of introduced larvæ, all the three-year-old ants to the number of twelve, all the two-year-old ants to the number of seventeen, all the one-year-old ants to the number of forty-two, and seven C nest ants of precisely its own age, so that the number of visitors arriving singly and at intervals amounted to eighty. A period of repose was provided after the removal of one visitor before another was introduced. Every one of these visitors was at first meeting violently attacked by this callow, dragged away from the larvæ, and in some cases taken outside the Petri cell, if I lifted its cover. Sometimes a visitor violently attacked the resident callow, and she had to be rescued by me from sudden death. In other like series of experiments with isolated callows the resident callow sometimes found a congenial odor in a visitor and willingly permitted her to share in the care of the larvæ.

Callows having their origin in different parts of the C colony area behaved alike, and it appears improbable that all of those tested could have been the product of eggs, larvæ or pupæ brought in by raids on another colony, especially when the greatness of the C colony is considered and its location studied.

Other experiments with callows from this colony gave support to my hypotheses. On July 11, 1904, there hatched in nest C₃, a pupa previously introduced by me from the C nest. I left it seven days with the three-year-old ants, and then transferred it to a Petri cell, giving it a few larvæ to care for. This isolated callow knew only its own odor, that of worker ants at least three

years old, and that of a queen. I then, a day or two later, introduced into its cell, one by one, all the one-year-old ants in nest C₁, removing each visitor as soon as the action of the resident was decisive, and allowing a period of repose before another visitor was introduced. She affiliated with the first, third, fourth, sixth, seventh, eighth, tenth and eleventh, and attacked the second, fifth and ninth.

I likewise introduced two-year-old workers from nest C₂. She affiliated with the first, third, fourth, fifth, seventh, ninth and twelfth, and attacked the second, sixth, eighth, tenth and eleventh. She did not attack the C₂ queen, but the queen so persistently avoided her as to make the test undecisive.

In the same manner I tested a callow, hatched on July 11, in nest C₂, where all the ants beside herself were two years old. When this callow had spent seven days in the C₂ nest, and one day in isolation with larvæ to care for, I introduced into her cell workers from the C₃ nest, where all the ants were three or more years old. She affiliated with the second, fourth, fifth, eighth, eleventh and twelfth, and attacked the first, third, sixth, seventh, ninth and tenth visitors. I then introduced one-year-old ants from nest C₁. She affiliated with the first, second, third, seventh, eighth, ninth, tenth and twelfth, and attacked the fourth, fifth, sixth and eleventh visitors.

I intended to likewise test a callow reared in nest C₁, and I expected to find that this callow would reject all three-year-old ants; but I unfortunately dropped an unmarked three-year-old ant into nest C₁, and thereby so vitiated the nest as to make it useless for this experiment.

A comparison of all the tests made gave a consensus of testimony that the C₃ ants, *the Stenammæ, recognized and adapted their behavior to ant-odors that they had not encountered during three years.*

As the workers are not supposed to reproduce colonies, and as the queens are not supposed to change their own odor, how then would queens of diverse odor originate through the ageing of the workers?

In 1901 I segregated winged queens of the C colony,¹ putting

¹ "Notes on an Ant," previously referred to, p. 605.

some of them into nests with kings of their own colony and others of them into nests with kings of alien colonies, and believed that I ascertained that the progeny of sister queens affiliated, regardless of paternal influence in the egg from which the ants issued. I then supposed that queen-ants captured before swarming must be virgin queens. I now know that virgin queen-ants often mate with the males within the maternal domicile, and that neither the possession of wings nor an early capture guarantee the virginity of a queen. Only by sequestration of the queen from her pupa-stage can her virginity be secured. I have had *Lasius latipes* queens drop their wings and lay eggs soon after being brought from the wild nest from which they had not yet swarmed. In my artificial nests, I have observed the persistent avoidance, by queens, of kings of alien colonies and their manifest preference for kings of their own colony. Mating in captivity, in artificial nests, is not uncommon, and it must be frequent in the wild nests before the swarming.

We know that the eggs of workers often produce sturdy males, and it appears probable that such males impart to the fertilized eggs of the queen something of the odor attained by the worker-mother at the time when the egg, producing the male, was deposited. This would differentiate odors in the progeny of sister queens, and cumulative differentiation would account for ultimate differences in the odor of queens of the same species and variety. When queens remain in the mother-nest after mating, and there rear their broods, that colony must become one of much mixed odors, as is the C colony described in this paper. Fertilized queens, departing from the maternal nest, would found colonies whose issuing queens would have an odor depending on the age of the workers who were mothers of kings hatched in the season in which their founder-queens mated.

Besides discerning the aura of the nest and other local scents and the track laid down by its feet,¹ an ant perceives in other ants the *incurred* or incidental odor which appears with conditions and disappears in course of time; the *inherited* odor derived from the queen-mother, apparent in the eggs, larvæ, pupæ and newly

¹ "Further Study of an Ant," A. M. Fielde, *Proceedings of the Academy of Natural Sciences of Philadelphia*, November, 1901, p. 521.

hatched young, and probably strengthening as size increases through the three inert stages of development; the *progressive* odor, that distinguishes the worker and changes or intensifies with her advancing age; and the *specific* odor which pertains to the species or tribe. Adding to these perceptions the power of recognizing familiar odors after a lapse of months or years, the ant appears to be well equipped for life in her world.¹ If she has not reason and imagination, she has at least the ground on which to exercise both, cognoscence of past experiences.

¹The organ discerning the nest-aura and probably other local odors lies in the final joint of the antenna, and such odors are discerned through the air; the progressive odor or the incurred odor is discerned by contact, through the penultimate joint; the scent of the track, by the antepenultimate joint, through the air; the odor of the inert young, and probably that of the queen also, by contact, through the two joints above or proximal to those last mentioned; while the next above these by contact also discerns the specific odor. It is probable that the size of the queen determines the amount of odor diffused by her. The amount of odor diffused by or discerned in the larvæ and pupæ may be the determining factor in the assorting of the young according to size, as is common among ants. The results of many experiments whereby the function of many joints in the antennæ were determined by me in 1901-1903 in *Stenamma fulvum* are recorded in "Further Study of an Ant" and "Cause of Feud among Ants of the same Species," above referred to. The joints in the antennæ vary in different species, from four to thirteen.